The physical factors in the growth of the tomato

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The tissues of animals and of the greater number of plants accumulate carbohydrates, proteins, salts and other solids during the course of growth in such manner that the relative dry weight of an organ is least in the embryonic or earlier stages, and increases progressively so that the proportion of solid material is highest and of water is lowest at maturity.

The stems and leaves of succulents and such berry-like fruits as the tomato (*Lycopersicum*) have been found to reverse this relation,* and melons, mushrooms and similar structures probably do the same.

Tomatoes 14–18 mm. in diameter grown at the Coastal Laboratory, Carmel, California, were found to contain but 87 per cent of water, while mature fruits consisted of 91 per cent water and 9 per cent solid material. An analysis by Albahary gave 93.63 per cent of water in young tomatoes and 94.3 per cent in ripe fruits.†

In addition to the measurements already published, it seems desirable to give the data secured in 1919, to make further comparisons between the apparent growth as found by the increase in the diameter of the fruits, and to record the actual increase in volume,‡ and to formulate an explanation of growth based upon the osmotic and colloidal action of the plasmatic substances under the influence of cell-sap of varying composition.

Vigorous plants bearing fruits in all stages were available in August and September, 1919, and suitable stages were erected

* MacDougal, D. T. Hydration and growth. Publ. Carnegie Inst. Washington, No. 297, 1920. See especially pages 166–172. Also, Hydration and growth, Proc. Amer. Phil. Soc. **58**: 346–373. 1919.

† Albahary, F. M. Etude chimique de la maturation du *Lycopersicum esculentum* (Tomate). Compt. Rend. Acad. Sci. Paris, **147**: 146–147. 1908.

‡ Note. In a discussion of this subject in the Proc. Amer. Phil. Soc. **58**: 367, 1911, the formula for obtaining the volume of a sphere, 4/3 (PiR^3) was erroneously given as (PiR^3).

so that small green fruits were resting securely on cork blocks. The vertical swinging arm of an auxograph also tipped with cork was now brought to rest on the upper surface of the fruit. Any variation in volume would be denoted by a deviation of the pen tracing from a horizontal line. A full description of this apparatus is given in connection with *f. 1* of the publication cited above.

The temperatures in this and in my other work on growth and swelling were taken by mercurial thermometers thrust into tissues or in contact with the bodies under observation. In the present instance small thermometers of the "clinical" type were thrust into fruits similar to those being measured and remained there during their development, causing but little divergence from normal morphology. The fruit stood between 15 and 20° C. during the experiments, which was on an average 8–10° below the optimum for these plants, but the relative humidity was favorably high.

The points to be presented may be demonstrated by the action of two fruits which were kept under continuous measurement, one for thirty-eight and the other for thirty-five days.

Fruit No. 1 had a diameter of 6 mm. and a volume of 113 cu. mm. when its measurement was begun, and its volume increased at the rate of 130 cu. mm. daily for six days, 402 cu. mm. for the following seven days, 409 cu. mm. for seven days, 560 cu. mm. for nine days and 930 cu. mm. for the last 9 days, at which time the total volume was 19,864 cu. mm.

The rate of increase of the diameter of these fruits during the same periods was 0.8 mm., 1 mm., 0.55 mm. and 0.6 mm. daily. A graph plotted from these daily rates would give a highly erroneous impression as to the actual course of accession of material to the fruits, which is the essential feature of growth. If the rate of growth be multiplied by twenty-five and placed in a table above the average daily increase in volume for the same period, a comparison may be made without the aid of a graph.

It is to be seen that the rate of increase in the diameter of the

Rate of increase	First week	Second week	Third week	Fourth week	Fifth week
Diameter	20	25	14	15	16
Volume	22	57	58	63	103

fruits at the maximum was not double the lowest rate, the highest occuring while the fruit was very small. Increase in volume, on the other hand, was progressively greater and as the fruit neared maturity water and material were being brought in nearly five times as fast as in young fruits. This delayed maximum might be connected with the low temperatures under which the development took place, as the highest rate of accession of material to fruits in 1918 at higher temperatures came somewhat earlier, although subsequent to the maximum increase in diameter.

A second fruit measured for thirty-five days was 8 mm. in axial diameter at the beginning and had a volume of 268 cu. mm. It increased 0.9 mm. in diameter and 167 cu. mm. daily for a week, 0.9 mm. daily for the second week with an accretion of 492 cu. mm., 0.7 mm. daily with an accretion of 412 cu. mm. in the third week, a rate of 0.67 mm. daily with an accretion of 1045 cu. mm. in the fourth week, and 0.3 mm. daily with an accretion of 600 cu. mm. in the last week.

A comparison of increases in diameter and volume is given below:

Rate of increase	First week	Second week	Third week	Fourth week	Fifth week
Diameter	27	27	21	20	9
Volume	27	56	59	150	185

The increase in diameter was at a rate which did not vary widely until at the last, when it dropped to less than half that which had previously prevailed. The rate of increase in volume rose steadily until at the end it was seven times as great as during the first week. The accretion is visualized as forming a layer on a globe, the volume of the fruit at any time being determined by the use of the formula $V = 4/3\ (PiR^3)$. A layer of a given thickness on a large fruit would obviously include a much greater amount of material than a layer of similar thickness on a small fruit.

The mechanical features of the growth of a storage body, as a fruit must be considered, are something different from those which prevail in a stem with its successively developing members or internodes, or in leaves which proceed to a definite average size

on maturity. In both types of growth the rate depends upon, or is influenced by, the amount of growth that has previously taken place, as has been demonstrated by Reed in his measurements of growth of the stems of apricot trees.

The stems of the tomato are enlarging during the growth of the fruits, the leaf surfaces are increasing and the pedicels of the fruits show an increasing cross section, so that not only is an additional amount of water and material available but its translocation may be facilitated.

It would be erroneous however to consider the fruits as reservoirs which passively receive the solutions poured into them through the stems. The fruits are in fact largely made up of rapidly enlarging masses of thin-walled cells which control absorption of material as occurs in living tissues. Liquids are drawn into these cells, not forced.

The forces which operate to carry water and solid material into a fruit may be grouped under osmosis and imbibition.

The freely soluble sugars which constitute about 9 per cent of the dry weight of young fruits and 38 per cent of ripe fruits, according to the analyses of Albahary, would operate to set up and maintain a turgidity that would probably reach eight to twelve atmospheres, and the attractive force of these substances would be one of the main factors in drawing material into the fruits.

It is well known, however, that fruits may withdraw water from stems that are relatively drier, and that roots may take up water from soils in which the osmotic action would be greater. To account for such action we must look to imbibition, the phenomena by which colloidal matter, such as jelly or wood, absorbs water or solutions and swells as a consequence of the hydration or addition of molecules of water to the aggregates of molecules of solid matter in their intimate structure, for growth under such circumstances.

Extensive investigations at the Desert Laboratory show that the living matter of plants is a mixture of albuminous substances and of pentosans or mucilages. Furthermore, parallel experiments with mixtures made in the laboratory show that in taking up water the plant behaves like a sac containing albumin and mucilages. It is necessary for a clear understanding of the action of the

plasmatic mass to realize that the albumin and mucilage may be taken to be in an interwoven meshwork, or if in suspension in separate globules.

This being the case, one may take up water and swell, or lose water and shrink, while the reverse action takes place in the other, which might also remain inactive. Thus the albumins swell most in acids or under the influence of free hydrogen ions, although being amphoteric they may also swell in hydroxyl ions or under the action of bases, while they are not very active in solutions of amino-compounds. The mucilages on the other hand are weak acids, swelling but little in acids, more under the action of hydroxyl ions or bases, still more in water, and reaching a maximum in amino-compounds.

Mixtures of mucilages and of albumins will, in the main, show reactions determined by the element which makes up the largest proportion of its mass. It follows therefore that the growing cell-masses of plants show swelling, hydration and growth reactions determined by the mucilages or pentosans, as modified by the albumins, acids, and salts present.

When we take up the facts disclosed by chemical analyses of tomatoes, we discover five things which must be taken into account in any attempt to make a physical-chemical explanation of growth These are as follows: (1) the proportion of sugar, including the mucilages, in the dry material increases from 9 to 37 per cent in the stage of enlargement including the formation of the seeds; (2) the acids, which include malic, phosphoric and citric, increase toward maturity; (3) the albumins decrease with development; (4) the ash or metallic bases increase from 4.5 to 10.75 per cent of the dry weight; and (5) the proportion of cellulose lessens as the fruit proceeds toward maturity.

If due weight be given to these factors or agencies the procedure in growth may be determined. Thus in the earlier stages the total albumins constitute less than 3 per cent of the dry weight and the sugars over 10 per cent, of which at least one third may be taken to be pentosans or mucilages. The colloidal mixture of equal parts of the two—mucilages and albumins—might be capable of showing a hydration capacity of over 3,000 per cent in a cell sap containing any one of a number of amino-acids which are

invariably present in cell-masses of this kind. The hydrogen ion concentration and the proportion of salts or bases is still low and their effect on the swelling would be limited. It would therefore be possible for these young fruits to make a notable amount of growth or expansion upon imbibition by the protein-pentosan plasma in a juice relatively low in salts and in acids.

Development and increase in size would however be attended by a lessened albumin content, making the plasma react more like agar in which hydration is lessened by salts and by acids, and imbibitional swelling would be notably decreased.

The accumulation of sugars in the cells occurring concurrently with lessened imbibition serves to set up an osmotic mechanism by which an increasing turgidity would result, serving as a distentive agency in the later stages of growth more than replacing the waning capacity for imbibition, and the action of osmosis in these fruits might have a heightened effect by reason of the fact that the cell walls of much of the fruit become "pectinated" and the proportion of cellulose becomes less, according to the analytical results of Albahary. This last named feature is the reverse of that in stems or vegetative tissues in which the cell walls become heavier and more indurated with progressive development.

The above conditions in the fruits are fully sustained by the following set of swelling reactions, which are entirely characteristic of a pentosan-protein colloid high in mucilages of the first group.

SWELLING OF RADIAL SLICES OF GROWING FRUITS 25–35 MM. IN DIAMETER

	Propionic acid	Alanine	Phenyl-alanine	Glycocoll	Water
0.01M	10%	25%	25%	25%	21%

In a later stage of the fruits when the skin is turning yellow, the salt content amounts to 10 per cent of the dry weight and the acidity is such that the sap has hydrogen ion concentration of a PH value = 4, while the albumins have decreased. The results of a set of swellings are as follows:*

	Propionic acid	Alanine	Phenyl-alanine	Glycocoll	Water
0.01M	16	15.5	11	15	15

* Cohn, E. J., J. Gross & O. Johnson. The isoelectric points of the proteins in certain vegetable juices. Jour. Gen. Physiol. 2: 145–160. 1919.

Regardless of other causes the acidity, high salt content and low albumin content would be sufficient to restrict absorption of water by the plasmatic colloids to two thirds the capacity shown by young fruits.

If we now turn to cultural experiments, ample confirmation is found for the conclusion that the amino-compounds which increase hydration or water absorption also facilitate or accelerate growth as measured in terms of dry weight, as found by Dachnowski and Gormley, Borowicov, Long, and Schreiner, Skinner and Beattie.*

Still one more feature of growth remains to be considered, that of certain retarding factors. The material which goes to increase the fruit of the tomato is about 90 per cent water. As water is being constantly transpired from the thin skins of these fruits, it is obvious that a hightened transpiration might throw off water at a rate which would use much of the liquid brought in by absorption and thus decrease growth. This occurs almost every day of sunshine and may result in the fruit having a lesser diameter at noon than at sunrise. Such cessation of growth in length and thickness of stems has been observed many times, and was earlier supposed to be due to the retarding action of light. It is however simply a loss of water greater than the absorption during the same time with a consequent shrinkage.

The principal conclusions supported by the foregoing may be briefly stated as follows:

1. The fruits of the tomato (*Lycopersicum*) furnish examples of development and growth without increase of dry weight.

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* See MacDougal, D. T. Hydration and growth. Carnegie Inst. Washington Publ. No. 297, 1920. See pp. 51 and 52, 63 and 64, and the following titles not considered in the preparation of that publication:

Schreiner, O., J. J. Skinner. Specific action of organic compounds in modifying plant characteristics; methyl glycocoll versus glycocoll. Bot. Gaz. **59**: 445–463. 1915.

Skinner, J. J., & J. H. Beattie. Effect of asparagin on absorption and growth in wheat. Bull. Torrey Club **39**: 429–437. *pl. 33.* 1912. (Good account of previous work with asparagin.)

Shreiner, O., & J. J. Skinner. Experimental study of the effect of some nitrogenous soil constituents on growth. Nucleic acid and its decomposition products. Plant World **16**: 45–60. 1913.

Borowicov, G. A. On the action of different substances on the velocity of growth of vegetables. Publ. Soc. Nat. New Russia **41**: 15–194. 1916.

2. The rate of increase in diameter of such globose, berry-like fruits is not a correct or even approximate measure of actual growth considered as an accretion of water and solid material.

3. The time at which the greatest increase in diameter takes place may coincide with the greatest growth as exemplified in previously described observations, but the increase in thickness is not a direct index of growth in such bodies. Actual growth varies as the cube of the radius.

4. The culmination of the rate may not be reached until the fruit is in a stage approaching maturity. The maximum accretion generally takes place in a stage subsequent to the highest rate of increase of the diameter.

5. The internal factors which determine the rate and amount of growth of the tomato include the soluble sugars and the salts or bases which increase toward maturity, and the albumins and celluloses which decrease with development, while the amino-acids, not determined, probably do not vary so widely as to affect their value as growth accelerators.

6. The conjunction of low acidity and low salt content and sugar content would give a set of conditions for high imbibitional swelling of a pentosan-protein plasma in the earlier stages of growth which would be capable of carrying the fruit to an enlargement of 3,000 to 4,000 per cent of the dry matter, as determined by previous experiments in the hydration of such colloids. Otherwise expressed, imbibition would be capable of making a colloidal body like a fruit which would consist of 97.5 per cent water and 2.5 per cent solid matter.

7. The higher salt content and acidity of older fruits would operate to lessen imbibition in the fruits, which in this stage would be high in carbohydrates.

8. The above facts support the conclusion that the distentive force in growth of young fruits is chiefly imbibition. Osmotic action may play the more important part in later stages.

9. The growth of a fruit therefore is a resultant of two groups of activities, one ordinarily classed as imbibitional and the other associated with osmosis and turgidity.

10. Young fruits include 1 to 4 per cent more solid material than mature ones, these bodies being representative of a type of

plant structure in which the dry weight does not increase with age.

11. The amino-acids induce a greater swelling or absorption of water by the cell masses of growing tomato fruits than takes place in weak acid solutions or in water. This fact is in agreement with, and is probably fundamental to, the accelerating effect of these substances on growth.

12. Continuous measurements of tomato fruits reveal slackened growth or shrinkage in the midday period corresponding to the time of greatest transpiration, and it is concluded that water absorption during this period is balanced by the loss from the surface, in accordance with the behavior of many other structures, such as trunks and twigs of trees, stems of sunflowers, joints of *Opuntia*, and leaves of *Mesembryanthemum*.

Desert Laboratory